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Cannibalism: A boon or a bane to fisheries

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Abstract

Cannibalism, the consumption of an individual of the same species, is prevalent in fish, but has only been reported for about 1% of the approximately 30,000 teleost fish in the sea and in freshwater worldwide. Some have suggested that cannibalism is an essential density-based regulatory mechanism; others have concluded that cannibalism has little or no importance for population dynamics. For some carnivorous fish, cannibalism is generally associated with several variables, such as heterogeneous size differences, limited food availability, high population density, limited protected areas and lighting conditions. There are many research possibilities to study how cannibalism is affected by the distribution of population size and ontogenetic differences in morphology and behavior, the structure of local communities, heterogeneity of habitat and abiotic environmental factors. The role of cannibalism in population dynamics remains controversial. Further research and a better understanding of cannibalism in fish, as well as the development of new techniques such as molecular methods, would not only help improve aquaculture, but also manage wild fish stocks and conserve species and mitigate the effects of invasive species.

Keywords: Cannibalism, types of cannibalism, intercohort cannibalism, intracohort cannibalism

Introduction

Cannibalism is a natural feeding strategy defined as the practice of eating one's own kind mentioned by Baras and Jobling (2002) ^[1]. Cannibalism, the act of intake an individual of the same species, has long attracted researchers and has been recorded for 390 teleost species, 104 families. In 1852, Hancock, reported a case of cannibalism by three Spine sticklebacks (*Gastrosteus aculeatus*, Gasterosteidae) in which a nesting adult consumed a juvenile that had approached it from another nest. In the classic paper entitled "stock and recruitment", Ricker (1954) emphasized the role of cannibalism as a density dependent regulator of fish population. Smith and Reay (1991) ^[32] concluded that cannibalism is common among teleost and discussed some of its causes and consequences. Most species with high rates of cannibalism reported from captive setting reveal little to no cannibalism in natural habitats (Fuentes and Quirked 2012). For example, captive dorada (*Brycon moorei*, Bryconidae) cannibalizes in early life stages (Baras *et al* 2000) ^[2]. Many fish species cannibalize early development stages. Species from the marine families Apogonidae, Gobiidae and Pomacentridae are primarily egg predators, usually involving filial cannibalism by beatings. Anchovies (Engraulidae) and other planktivorous fishes sometimes consume eggs of conspecifics, and presumably, most of them are unrelated. Species of Bryconidae, Cyprinidae, Pimelodidae, Poeciliidae (freshwater families) and Serranidae (marine) feed almost exclusively on larval stages, and Merlucciidae (marine) and Salmonidae (freshwater and anadromous) feed mostly on juveniles. Cannibalism is dominated in a few freshwater fish families: Percidae (140 occurrences, with *Perca fluviatilis* and *P. flavescens* most frequent), Salmonidae (75 occurrences, with *Salvelinus alpinus* most frequent) and Esocidae (54 occurrences, with *Esox lucius* most frequent) and marine families Gadidae (106 occurrences, with *Gadus morhua* most frequent), Gobiidae (54 occurrences with *Pomatoschistus microps* most frequent) and Merlucciidae (29 occurrences). Smith and Reay (1991) ^[32] found that cannibalism was most common in piscivorous fishes. Cannibalism may result from high conspecific density in combination with low prey diversity and abundance. Cannibalism by non-carnivorous species, eg., those that feed on algae, plants or detritus, was rarely reported in nature and the three cases of partial filial cannibalism were reported for two herbivorous Pomacentrids (Petersen 1990) and one detritivorous Gobiid (Hernaman *et al.* 2009) ^[13]. Filial cannibalism was observed for 55 species, of which 25 involved in captive settings. Eggs in the development stage most frequently cannibalized, and this behavior is observed in diverse feeding guilds.

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Parents can consume either the entire clutch (total filial cannibalism) or only a few eggs (partial filial cannibalism), with the former viewed as an investment in future reproduction, whereas the latter influences both current and future reproductive success (Sargent 1992) ^[31]. Total filial cannibalism is expected when the cost of care is high, and may be influenced by brood size and age, parental body condition, local abundance of males, and degree of certainty of paternity (Kondoh and Okuda 2002; Manica 2004) ^[14, 21]. Captive Egyptian mouthbrooders (Multicolor Pseudocrenilabrus; Cichlidae) swallowed all remaining eggs from their clutch if their number dropped below 20 percent of the initial number (Mrowka 1987) ^[23]. *Telmatherina sarasinorum* (Telmatherinidae), nest guarding male cannibalized eggs when there was cuckoldry (Gray *et al.* 2007) ^[12]. When confronted with cuckoldry, nesting male bluegill sunfish (*Lepomis macrochirus*, Centrarchidae) adjusted parental care to favor broods more closely related to the male (Neff 2003) ^[25]. The presence of sneaker males during spawning can reduce certainty of paternity (Neff and Gross 2001; Neff and Sherman 2003) ^[24, 26]; however, once the eggs hatch, the male can use chemical cues to differentiate its offspring released by the fry (Brown and Brown 1996; Neff and Sherman 2003, 2005) ^[3, 26, 27]. In addition, some eggs generally are not fertilized, and these are selectively consumed a few days after spawning (Mrowka 1987) ^[23]. Filial egg cannibalism is usually restricted to males, possibly because males can gain significant additional energy, whereas females that consume their own eggs cannot regain all of the energy expended in gamete production (Kondoh and Okuda 2002, Manica 2002, 2004) ^[14, 20, 21]. Parental nutritional status (body condition) has been shown to influence filial cannibalism (Kondoh and Okuda 2002; Manica 2002, 2004) ^[14, 20, 21]. Energetic costs associated with parental care, mainly in the form of egg fanning, together with reduced feeding opportunities may cause deterioration of the male's physical condition (Marconato *et al.* 1993) ^[22]. One potential response to reduced feeding opportunities during parental care is cannibalism of embryos (Rohwer 1978) ^[30]. Brood-guarding males, in particular, exhibit greater frequencies of cannibalism with declining body condition (Okuda and Yanagisawa 1996). Egg cannibalism could be a strategy primarily for obtaining energy as opposed to essential dietary nutrients (Svensson *et al.* 1998). The number of eggs eaten by male bullheads (*Cottus gobio*, Cottidae) was positively correlated with the number of egg masses in the nest (Marconato *et al.* 1993) ^[22], possibly due to greater energy demand for care of larger broods. Egg cannibalism by males can also be influenced by female behavior. Garibaldi damselfish (*Hypsypops rubicundus*, Pomacentridae) males tend to cannibalize older eggs, apparently because females prefer to spawn with males guarding early-stage eggs rather than those guarding later stages. This runs counter to the assumption that older eggs possess higher reproductive value than younger eggs, and parents should therefore suffer greater fitness deficit by consuming older eggs (Fitzgerald 1992; Sargent 1992) ^[10, 31]. For species with brood care, egg cannibalism can account for more than 90% of the energy required for reproduction.

Types of Cannibalism

A classification of fish cannibalism has not hitherto been available. However, on the basis of three distinct criteria, classification have been formulated which reflects the full range of cannibalistic events in fish. The first criterion is the

stage of development of the prey, cannibalism being directed either at the egg or at post-hatching stages. In egg cannibalism the prey is passive, since eggs clearly exhibit no escape reaction. In contrast, cannibalism of larval, juvenile or adult stages demands some degree of active predation, although there must be a period of variable duration after hatching when predation on larvae will be no more demanding than predation on eggs. The second criterion defines the genetic relationship between cannibal and prey. Distinctions are drawn between cannibalism by a parent on its own offspring (filial cannibalism), of one sibling on another (sibling cannibalism) and between unrelated individuals (non-kin cannibalism). In many situations, particularly in field studies, the degree of relatedness is unknown, and it has to be assumed that individuals are unrelated. Cannibalism is lastly distinguished with respect to the relative ages of cannibal and prey.

Intracohort cannibalism is considered here where cannibals and prey belong to the same annual age cohort, and intercohort cannibalism occurs when the cannibal belongs to an older cohort. On the basis of these criteria, cannibalism in teleosts falls into six classes, with one further class represented so far only by chondrichthyan fish. This classification shows that cannibalism in fish is not without some pattern. Also, imposing a classificatory structure on a largely overlooked aspect of fish behaviour will facilitate a more integrated approach to the subject. Terms adopted for this classification have been selected on the basis that they provide the best, and least ambiguous, descriptions of a particular criterion; where possible, terms already used in the scientific literature have been retained, e.g. 'filial cannibalism'. One term in occasional use is replaced. This is 'heterocannibalism' (renamed non-kin cannibalism), which comes from Rohwer.

Filial Intercohort Cannibalism of Eggs

Surprisingly, consumption of filial eggs in fish is not uncommon, and 25 species have been identified as doing so. It has been attributed to disturbance in care-giving cichlids studied by Eyeson, (1983) ^[7], failure to elicit parental behaviour in belontiids reported by Kramer, (1973) ^[15] and, in female *Gasterosteus aculeatus* (Gasterosteidae), to the attempt to recoup somatic losses by participating in attacks on their own eggs according to FitzGerald and van Havre, (1987) ^[9]. In species exhibiting parental care, filial egg cannibalism may also be a response to reduced foraging opportunities during the care period observed by Rohwer, (1978) ^[30].

Sibling Intracohort Cannibalism of Eggs

An example of this class of cannibalism has not been located for teleost fish, though it is not inconceivable for nest-building or viviparous species. Among odontaspimid and lamnid elasmobranchs, 14 species are known to exhibit intrauterine oophagy mentioned by Wourms *et al.*, (1988) ^[36], conspecific eggs serving as food for developing embryos. An osteichthyan, *Latimeria chalumnae* (Latimeriidae), also appears to exhibit this form of cannibalism reported by Wourms *et al.*, (1980) ^[35], as did an extinct holocephalan, *Delphyodontos dacrifomes* according to Lund, (1980) ^[19].

Non-Kin Intercohort Cannibalism of Eggs

The majority of identified cases of egg cannibalism are attributed to non-kin intercohort cannibalism, as exemplified by the Engraulididae (Valdes *et al.*, 1987) ^[33]. It is typical

both of filter-feeding marine planktivores and of freshwater and marine species in which non-breeding, and Dominey, (1981a)^[4] observed often immature fish invade spawning or nesting areas to feed on eggs, e.g. *Lepomis machrochirus* (Centrarchidae).

Filial Intercohort Cannibalism of Post-Hatching Stages

Only seven instances of this class of cannibalism have been identified. One example concerns the live-bearing females of *Poecilia spp.* (Poeciliidae), which are notorious cannibals of filial young, at least in captivity observed by Fahrig, (1972)^[8]. Loekle *et al.* (1982)^[18] provided evidence of recognition of offspring by female *Poecilia spp.*, these fish avoiding cannibalism of their own fry while readily attacking unrelated young. In this species at least, filial intercohort cannibalism of post-hatching stages is discrete from non-kin intercohort cannibalism.

Sibling Intracohort Cannibalism of Post-Hatching Stages

The cannibalism of siblings belonging to the same age cohort is a characteristic of piscivorous species during early stages of development. The ability to eat siblings in early life, before brood dispersal, is facilitated by a large gape and well-developed teeth at, or soon after, hatching as in *Esox lucius* (Esocidae) observed by Giles *et al.*, 1986)^[11]. A group of siblings of a non-predatory species can also exhibit this class of cannibalism if prevented from dispersing (e.g. under aquarium conditions), and after sufficiently large size differences have evolved due to differing growth rates, e.g. *Cyprinus carpio* (Cyprinidae) reported by Damme *et al.*, (1989)^[34].

Non-Kin Intracohort Cannibalism of Post-Hatching Stages

Like sibling intracohort cannibalism, this class is common to piscivorous species in early life, e.g. *Stizostedion v. vitreum* studied in Li and Mathias, (1982)^[17]. It is also found in all fish groups in which large size differences become established within age cohorts, and consequently it represents a problem in aquaculture, e.g. *Oreochromis niloticus* observed in Pantastico *et al.*, (1988)^[28].

Non-Kin Intercohort Cannibalism of Post-Hatching Stages

Predation by older and unrelated conspecifics accounts for the majority of cases of cannibalism in fish, this review having identified 62 species indulging in such behaviour; *Theragra chalcogramma* (Gadidae) reported by Dwyer *et al.* (1987)^[5] provides a good example.

Conclusion

Given the growing emphasis on aquaculture to increase food supply, research is clearly needed to reduce cannibalism among fish held at high densities in captivity. At the same time, the commonness of cannibalism and its causes and consequences for fishes in nature remain poorly understood. Cannibalism has been described as being widespread in fish (Smith and Reay 1991)^[32], and yet it has been reported for only about 1% of the approximately 30,000 marine and freshwater teleost fishes worldwide mentioned by Leveque *et al.* (2008)^[16], with most accounts from aquaculture settings. One might then ask—why are there so few reports of fish cannibalism?

Eigaard *et al.* (2014)^[6] found the absence of field

observations on cannibalism in fish surprising, since most fish have external fertilization, pelagic larvae and reproductive strategies that favor offspring quantity rather than the size of the offspring. Perhaps cannibalism actually is rare among wild fishes, and occurs only when there are occasional opportunities. Most fish may rarely encounter small conspecifics or are incapable of pursuing, capturing and ingesting them or perhaps cannibalism is more common than indicated by currently available evidence. Dietary studies may fail to document cannibalism due to inadequate methodologies or lack of interest to search for it. Perhaps most species have evolved effective mechanisms to avoid cannibalism because it reduces inclusive fitness. On the other hand, there is new evidence that cannibalistic behavior has a genetic component, which suggests a potential fitness advantage. The role of cannibalism in population dynamics is still controversial. Some have proposed that cannibalism is a critical mechanism of density dependent regulation, but others have concluded that cannibalism has little or no importance for population dynamics. Many research opportunities exist for addressing how cannibalism is influenced by population size distributions, ontogenetic variation in morphology and behavior, local community structure, habitat heterogeneity, and abiotic environmental factors. In addition to ecological modeling, comparative field studies and controlled lab and field experiments are needed to address these questions. Our review found evidence of cannibalism in hundreds of fish species, including many accounts from wild populations, but this represents a tiny fraction of global fish species richness. Much more effort is required to overcome the many potential sources of biasing the current body of evidence. For example, eggs and larvae, the stages most vulnerable to predation by conspecifics, are difficult to identify visually to species level during stomach contents analysis, and are digested even more rapidly than small fish. Development of new techniques, such as molecular methods, would greatly improve estimates of predation on early life stages. Better documentation and understanding of fish cannibalism would contribute not only to improved aquaculture, but also to management of wild fish stocks, conservation of threatened species, and mitigation of impacts from invasive species.

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